

Continental Shelf-Wide Response of a Fish Assemblage to Rapid Warming of the Sea

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Summary

Climate change affects marine biological processes from genetic to ecosystem levels [1–3]. Recent warming in the northeast Atlantic [4, 5] has caused distributional shifts in some fish species along latitudinal and depth gradients [6, 7], but such changes, as predicted by climate envelope models [8], may often be prevented because population movement requires availability of suitable habitat. We assessed the full impacts of warming on the commercially important European continental shelf fish assemblage using a data-driven Eulerian (grid-based) approach that accommodates spatial heterogeneity in ecological and environmental conditions. We analyzed local associations of species abundance and community diversity with climatic variables, assessing trends in 172 cells from records of >100 million individuals sampled over 1.2 million km² from 1980–2008. We demonstrate responses to warming in 72% of common species, with three times more species increasing in abundance than declining, and find these trends reflected in international commercial landings. Profound reorganization of the relative abundance of species in local communities occurred despite decadal stability in the presence-absence of species. Our analysis highlights the importance of focusing on changes in species abundance in established local communities to assess the full consequences of climate change for commercial fisheries and food security.

Results and Discussion

Average global sea surface temperature (SST) increased by 0.7°C over the last 100 years [4] and is predicted to rise by

a further 1.5°C to 2.6°C by 2100 [9]. Marine ecosystems in the northeast Atlantic have warmed particularly rapidly, with mean sea temperatures in the North Sea and Celtic-Biscay Shelf regions increasing between 1982 and 2006 by 1.31°C and 0.72°C, respectively [5], four times faster than the global average [4]. Climate warming is affecting marine biological processes from the genetic to ecosystem level of organization, with implications for commercial fisheries and food security [1–3]. Significant progress has been made with identifying mechanisms by which climate change can affect fish population dynamics [10, 11] in describing shifts in the distributions of some fish species along latitudinal and depth gradients associated with climate change [6, 7, 12] and in developing climate envelope models to predict effects of climate change on future species distributions [8]. To date, however, macro-ecological analyses of the effects of climate change on marine fish assemblages have not accounted for constraints on distributional shifts due to population dependence on essential habitat, for example, favored substrates, appropriate predator and prey fields, and close proximity to nursery grounds, all of which are often unknown and difficult to quantify. Accommodation of spatial habitat heterogeneity when measuring climate impacts requires an alternative Eulerian (grid-based) approach of analyzing multiple local associations of species abundance and community diversity with climatic variables, controlling for depth and latitude and allowing for complex oceanography.

To investigate the effects of temperature variability on abundance of demersal species within the European continental shelf fish assemblage, we compiled and analyzed three decades of high-resolution fisheries-independent data. Our analysis spanned ~1.2 million km² of seabed (15° latitude × 25° longitude) and depths ranging from 5 to 592 m (mean = 75 m) and used data from 25,612 bottom-trawl sample hauls between 1980 and 2008 comprising >100 million fish from 177 species (or species groups; see [Tables S1 and S2](#) available online). Temperature in this region has increased by 0.06°C years⁻¹ on average at the surface and by 0.04°C years⁻¹ on the seabed during the past 30 years ([Figure 1A](#)). Significant warming trends were evident in all 172 1° × 1° cells within the region and were most intense in the southern and eastern North Sea and the Irish Sea ([Figure 1B](#)). Trends in SST and sea-bottom temperature (SBT) correlated closely (Pearson's $r = 0.94$, $p < 0.001$), whereas there was no significant correlation between regional rates of fishing mortality (another key driver of trends in fish abundance) and temperature (SST: $r = -0.29$, $p = 0.16$; SBT: $r = -0.13$, $p = 0.56$), which increased during the 1980s but declined thereafter [13] ([Figure 1A](#)).

Stability in Species Composition in Communities Despite Warming

An unsupervised Bayesian clustering analysis using species presence-absence data identified 12 biogeographic clusters across the studied shelf region ([Figure 2A](#)). The distribution of these clusters was generally stable between consecutive 5 year time periods, although during the period of the most rapid warming in the late 1980s ([Figure 1A](#)), more than twice as many cells changed in identity between 5-year periods

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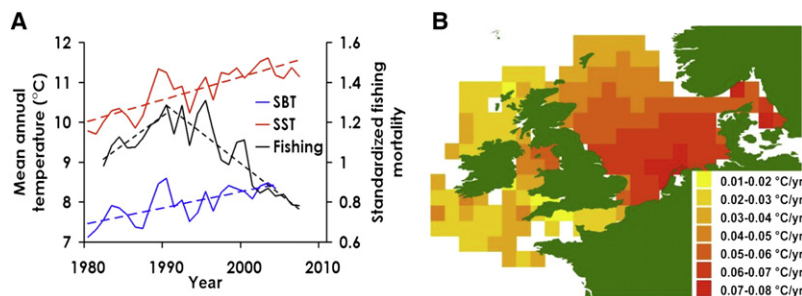


Figure 1. Environmental Conditions on the European Continental Shelf

(A) Temperature and fishing trends. Annual temperature trends are calculated for the $1721^{\circ} \times 1^{\circ}$ cells in this study and are shown with a linear trend (sea surface temperature [SST]: $+0.06^{\circ}\text{C years}^{-1}$, $R^2 = 0.67$; sea-bottom temperature [SBT]: $+0.04^{\circ}\text{C years}^{-1}$, $R^2 = 0.50$). Standardized fishing mortality is the mean estimate of multispecies fishing mortality for six subregions (North Sea, Eastern Channel, Western Channel, Celtic Sea, Irish Sea, Northwest Scotland) weighted by the spawning-stock biomass of each species that is assessed, as reported in International Council for the Exploration of

the Sea working group reports and is shown with two linear trends (1982–1990: $R^2 = 0.80$; 1990–2007: $R^2 = 0.81$).

(B) Spatial variation in temperature trends during the study period (1980–2008), expressed as the slope of a fitted linear relationship between SST and year for each cell.

compared with the 1990–2000s (Figure S1). In total, 53% of cells changed identity at some time during the 30 years, but only four of the 12 clusters changed significantly in latitudinal distribution. The western central North Sea and Channel assemblages moved southwards and the southeastern North Sea and Irish Sea clusters moved northwards. The spatial patterns of clusters were not driven by rare species (Figure S2) and were not associated with boundaries between different surveys. Instead, similar patterns were seen in regional analyses of data from single surveys (Figure S3). Thus, the general pattern on the European continental shelf is one of relative stability of overall species presence-absence, despite ubiquitous recent warming, a pattern that concurs with an earlier study of North Sea fish that found no overall consistent trend in latitudinal shifts among the 36 species studied [6]. Together, these analyses suggest that management zones based on biogeographical criteria [14] are acceptable on longer

timescales than implied by reports of changing distributions due to recent warming [6].

Seventy-Two Percent of Common Species Are Responding to Warming

Observations of latitudinal shifts of some North Sea species over decadal timescales [6] raise questions about how changes in abundance relate to changes to species distributions. Across the region, we identified significant positive associations between fish annual abundance and temperature for 27 of the 50 most abundant species, whereas nine species showed significant declines in abundance relative to warm years (Figure 3; Table S2). The mean central latitude (derived from FishBase [15]) of the 27 species that increased in relative abundance with warm conditions across the region (44.5°N ; Table S2) was significantly lower than the nine species that declined (55.2°N ; t test [equal variances not assumed],

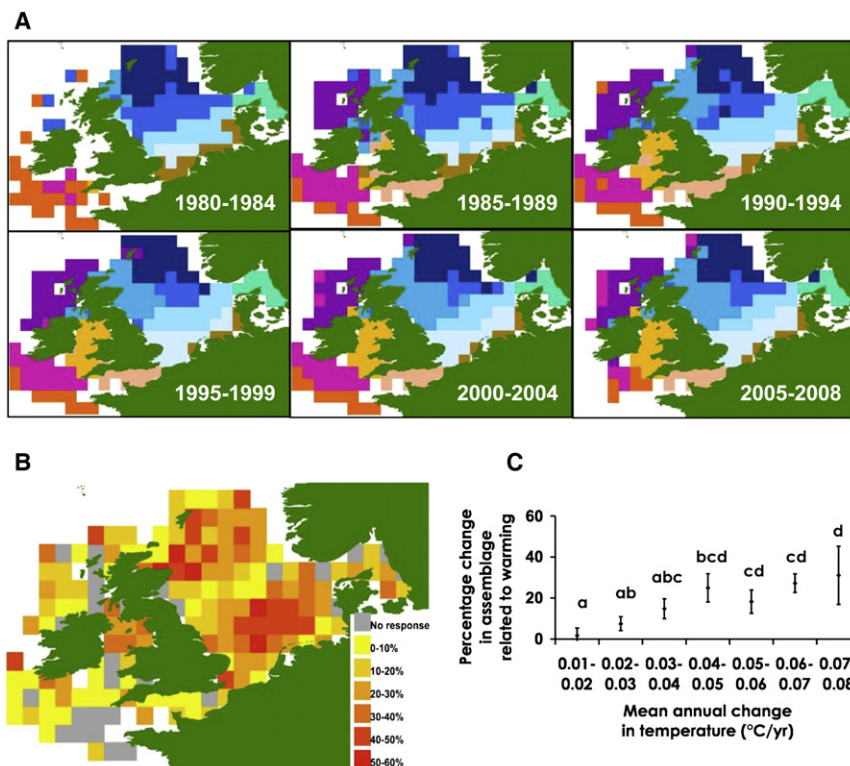


Figure 2. Assemblage Composition in Relation to Warming

(A) Twelve biogeographic clusters, identified by Bayesian analysis of presence-absence data, that maintained similar distributions over six 5-year periods. White cells in (A) and (B) indicate locations with insufficient fish-abundance data. (See Supplemental Information for further analysis of cell cluster changes [Figure S1], patterns based solely on common species [Figure S2], and patterns within single surveys [Figure S3].)

(B) Eighty-two percent of cells with a positive assemblage response to warming (percentage variation above random in beta-diversity trend explained by temperature). (See Figure S4 for comparison of trends with different temperature measures.)

(C) Mean assemblage response to temperature within $1^{\circ} \times 1^{\circ}$ cells classified by intensity of warming. Letters above 95% confidence interval bars indicate significantly different categories (analysis of variance, $F_{6,162} = 9.865$, $p < 0.001$; subgroups identified using Tukey's honestly significant difference test, $\alpha = 0.05$).

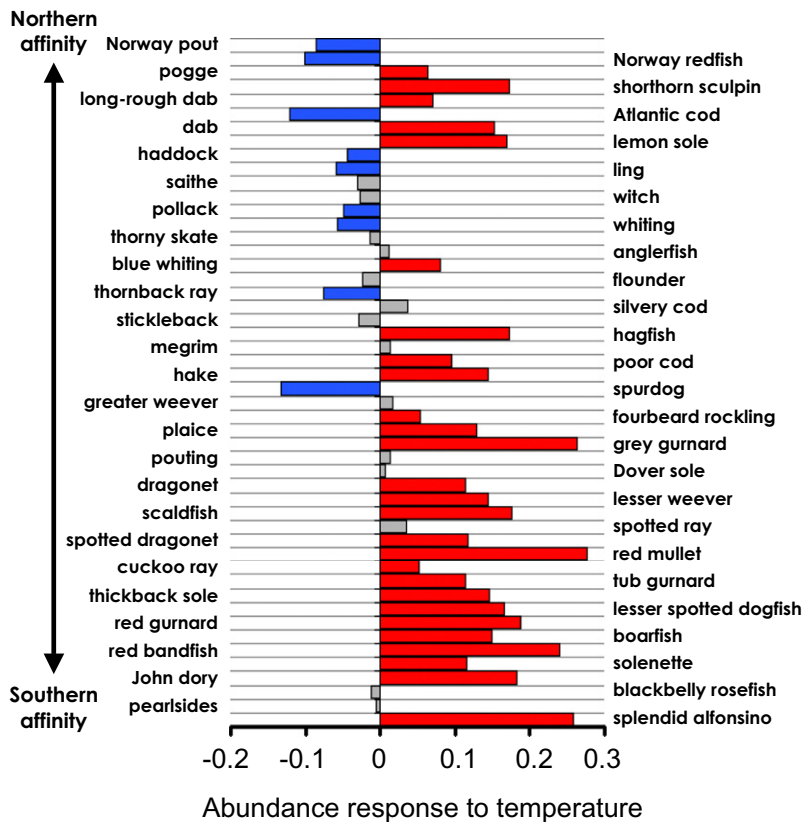


Figure 3. Species Abundance Responses to Warming
Mean species-level relationships between abundance and temperature for the 50 most common species in $172 1^\circ \times 1^\circ$ cells. Red indicates an increase in abundance in warm years, blue indicates a decline, and gray indicates no significant response. (See Table S2 for scientific names, species life history traits, and regional-scale responses.)

determining and predicting abundance responses of species to warming seas.

International Commercial Landings Reflect Abundance Changes

Although commercial landings data may give biased estimations of natural abundance [17], they give a valuable indication of the importance of species to the fishing industry. We investigated whether commercial landings [18] of species from northeast Atlantic fisheries reflected the abundance response of species to warming over the last 30 years derived from fisheries-independent data. There was a significant positive relationship between the trend in commercial landings (between 1980 and 2007) and the abundance response to temperature from survey data for the 33 species for which fisheries data were available (Pearson's $r = 0.41$, $p = 0.018$; Figure 4C). There was also a positive relationship between preferred temperature of species in

surveys and landings trend ($r = 0.51$, $p = 0.002$) and a negative relationship between central latitudinal range and landings trend, with higher latitude species declining in landings ($r = -0.57$, $p = 0.001$). These results indicate that observed changes in survey data are mirrored in landings of commercial species.

Local-Scale Reorganization of Communities across the Region

Finally, we investigated whether changes in local assemblage composition have occurred despite stability in species presence-absence. We used principal component analysis (PCA) to reduce matrices of species abundance data for each year in each $1^\circ \times 1^\circ$ cell and used principal component 1 (PC1) as a single metric summarizing the major temporal trend in beta-diversity in subsequent analyses [19]. On average, PC1 captured 34% of variation within cells (range 20%–74%), and mean annual SST with a 1 year time lag explained more variation in PC1 than expected by chance in 143 of the 172 cells (Figure 2B). Annual SBT with a 1 year lag explained more variation than expected by chance in 131 cells. This stronger association of surface temperature with fish assemblage change may indicate that temperature exerts its effect via pelagic larval stages. At a $1^\circ \times 1^\circ$ resolution, neighboring cells often had contrasting assemblage responses to warming, implying differential effects of local habitat and/or interspecific ecological interactions [19]. Temperature-driven changes in assemblage composition were most pronounced in the southern and northern North Sea and the Irish Sea (Figure 2B), matching warming hotspots (Figure 1B). Assemblage-level change was significantly greater in cells that have experienced more intense warming (Figure 2C), and the reduced response

$t_{24,3} = 4.33$, $p < 0.001$). This difference held for the central latitudinal tendency of these species when calculated from the main data set (53.5°N versus 55.3°N , $t_{14,5} = 2.58$, $p = 0.021$). Generally, central latitudinal range was significantly correlated with the abundance response of species to warming (Pearson's $r = -0.52$, $p < 0.001$; Figure 4A), and this relationship was also apparent using the central latitudinal tendency of each species within the data set ($r = -0.44$, $p = 0.001$). Although preferred temperatures of species (mean temperature at capture of all individuals) that increased in abundance with warm conditions (mean = 11.3°C) were not significantly different from those of species that declined (mean = 10.8°C , $t_{21,6} = 1.66$, $p = 0.112$), there was a significant overall correlation between preferred temperature and abundance response of species to warming ($r = 0.31$, $p = 0.027$; Figure 4B). Maximum body size provides a proxy for ecological performance, as well as other life history parameters, demography, production, consumption, and metabolism [7, 16], and the 27 species that were more abundant during warm conditions (mean = 493 mm) were significantly smaller than the nine species that declined (956 mm, $t_{9,709} = -3.20$, $p = 0.01$). However, maximum body size was not directly correlated with the strength of response of species to warming ($r = -0.147$, $p = 0.309$). There was also no significant difference in depth preference of species (mean depth at capture of all individuals) that increased in warm conditions (mean = 99 m) from those that declined (mean = 108 m, $t_{31,70} = -0.92$, $p = 0.364$) and no overall relationship between preferred depth and index of response ($r = 0.02$, $p = 0.892$). In combination, the results from this analysis indicate the importance of overall latitudinal occurrence and temperature preference, but not depth preference, in

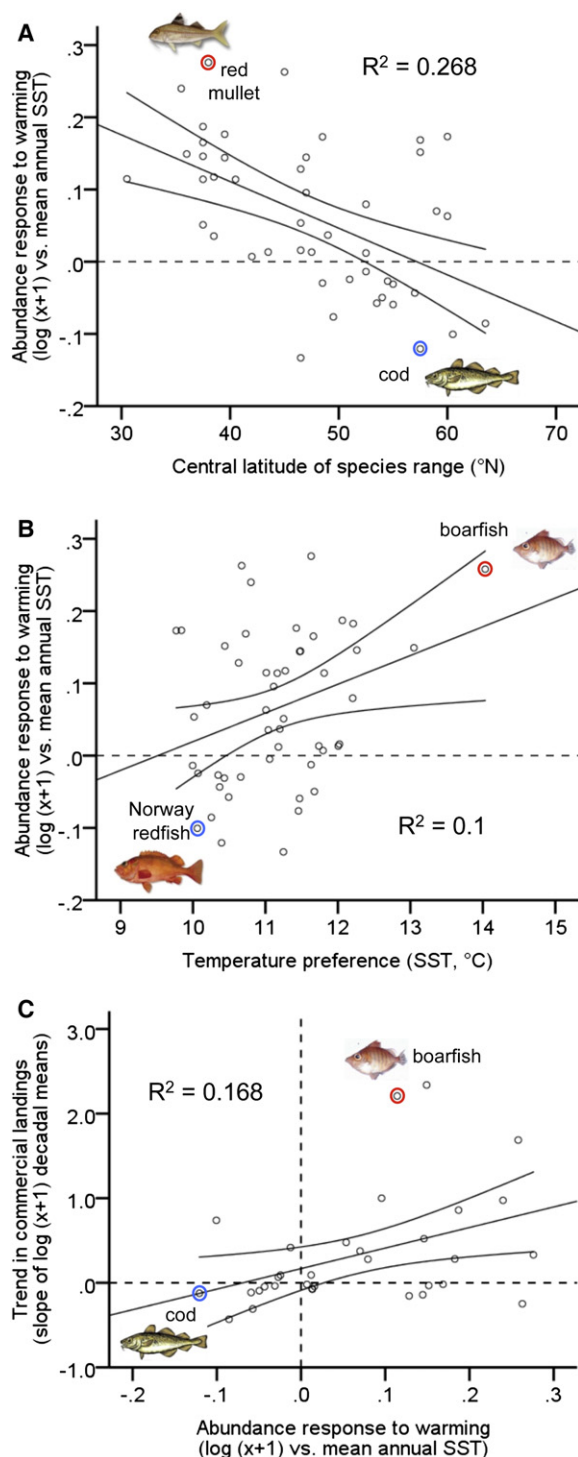


Figure 4. Species Responses to Warming and Impact on Fisheries
(A and B) Abundance response of species to temperature for the 50 most common species in relation to species characteristics: mean latitude of occurrence (A) and preferred temperature (B).
(C) Increase in commercial landings of species with positive abundance responses to warming and decline in landings of species with negative responses.

for cells with lower levels of warming suggests resilience to warming to a threshold, beyond which change becomes inevitable and pronounced.

Conclusions

The results here are unique in exploring observed spatial heterogeneity in the response of the assemblage at a resolution that matches the one used in climate envelope models [20]. Our finding of stability in presence-absence of species over decadal periods, but significant temperature-driven responses in local species abundance and assemblage composition, suggests that climate envelope models based on species presence-absence alone will not predict the most ecologically and economically significant effects of climate change. Moreover, studies exploring shifts in central latitudes of species ranges using abundance data may miss important spatial variability and local responses. For example, poleward shifts in abundance, as would be expected under climate envelope scenarios, have been identified in only 13 of 36 studied species (36%) in the North Sea assemblage [6] despite significant and ubiquitous changes in temperature. In contrast, by analyzing local changes in abundance without assuming a range shift during warming and allowing for uneven abundance distributions linked to suitable habitat, we identified temperature-associated species-level changes in abundance in the North Sea in 39 of the 50 (78%) most common species (Figure 3; Table S2) and identified change in assemblage composition associated with warming in 93% of the North Sea cells (Figure 2B). This is consistent with many species responding in abundance without necessarily changing their spatial distributions of occurrence within the study region. The impact of these abundance changes to commercial fisheries was apparent, where landings of the nine species identified as declining in warm conditions (blue species in Figure 3, including haddock and cod) fell by a half during the period of this study, whereas landings of the 27 species identified as increasing in warm conditions (red species in Figure 3, including hake and dab) increased 2.5 times. For a given region, reorganization of the fishing fleet and management strategies will be required to ensure that the right species are targeted and harvested sustainably.

Our analysis highlights the value of data from high resolution large-scale surveys of species abundance in regions with a known history of climate change. The focus of many studies on the ecological effects of climate change in marine fish or fisheries has been on changing abundance distributions along latitudinal or depth gradients. Our analyses demonstrate that such distributional changes have been relatively benign on the European continental shelf during rapid warming of the sea over the last 30 years. Instead, there has been profound climate-driven reorganization of species abundance in established local communities over much of the shelf region, without spatial reorganization of species presence-absence. This result is important because local abundance changes in established fish communities have the greatest implications for both ecosystem function and societies dependent on marine natural resources. By contrast, over the timescale, studied changes in species ranges are arguably less important, because they result only from colonizations or extirpations that occur when species are necessarily scarce and below the abundances required for commercially viable exploitation. Thus, studies of distributional shifts can overlook ecologically and economically significant climate effects, except for rare examples of species range expansion coupled with large increases in abundance (e.g., [21]). The next challenge is to use this knowledge to develop effective indicators and predictive models to assess consequences of climate change for marine ecosystems and

fisheries. Such models will need to consider growth, reproduction, habitat use, essential habitat requirements, and location of nursery and spawning grounds if they are to make predictions about likely future impacts of warming on food web dynamics and fish-driven ecological processes. Moreover, because the northeast Atlantic assemblage is heavily exploited and species responses to fishing are influenced by body size [22], models are needed that integrate effects of warming and fishing. This gained understanding will be valuable for predicting future exploitable resources and crucial for determining appropriate harvesting and conservation strategies at relevant spatial scales.

Experimental Procedures

Data were collated from 11 demersal trawl surveys conducted over 30 years by European fisheries agencies in $218\ 1^\circ \times 1^\circ$ cells (Table S1). The combined data comprised 25,612 hauls and an estimated 105,304,825 fish from 177 species or taxa in 172 cells. Bathymetry data were obtained from General Bathymetric Chart of the Oceans [23]. Modeled SST [24] and SBT [25] data used to describe warming trends correlated closely with in situ measurements (Pearson's correlation; SST: $n = 5,666$, $r = 0.94$, $p < 0.001$; SBT: $n = 2,789$, $r = 0.78$, $p < 0.001$) from the 22% and 11% of hauls for which they were available, respectively. International Council for the Exploration of the Sea stock assessment data [26] were used to calculate weighted multispecies estimates of fishing mortality [27] for each International Council for the Exploration of the Seas region. Unsupervised Bayesian clustering [28] of presence-absence data for six 5 year time periods identified biogeographically distinct subassemblages. Abundance responses of species to temperature were calculated for the 50 most abundant species (comprising 99.9% of individuals sampled) as the mean correlation coefficient for all cells between catch and temperature data. For each species, we determined biogeographic affinities from within our data set and using the central latitudinal range from FishBase [15] and obtained maximum body size from all records in the trawl survey database (Table S2). Preferred temperature and depth for each species were derived using frequency of occurrence across the data set. We defined an assemblage-level response to temperature for each $1^\circ \times 1^\circ$ cell as the association above that expected by chance between PC1 from a PCA of a matrix of log abundance (per species per year) that associated with mean annual SST from the previous year. This was identified as the best predictor from 18 potential drivers for each cell (SST and SBT; annual, summer, and winter; 1–3 year time lag; Figure S4).

Supplemental Information

Supplemental Information includes four figures, two tables, and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2011.08.016.

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